

A REVIEW OF THE FROND-LIKE FOSSILS OF THE EDIACARA ASSEMBLAGE

by

RICHARD J. F. JENKINS* and JAMES G. GEHLING†

ABSTRACT

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*Centre of Precambrian Research, University of Adelaide, Adelaide, South Australia 5000.

†Murray Park College of Advanced Education, 15 Lorne Avenue, Magill, South Australia, 5072.

Restudy of the frond-like fossils which occur as part of the Late Precambrian, Ediacara assemblage of the Flinders Ranges confirms previous reconstructions which show the majority of these forms to be basically foliate, leaf-like structures. In some, the axial zone or rhachis terminated in a disc-like anchoring device.

The genus *Arborea* Glaessner and Wade, 1966, is considered a synonym of *Charniodosaurus* Ford, 1958, and a new species of this genus is described. The genus *Glaessnerina* Germs, 1973, is briefly reviewed and earlier opinion that *Charniodosaurus* and *Glaessnerina* are probably related to the extant Pennatulacea is confirmed. *Phyllozoon hansenii* gen. et sp. nov. is a new taxon resembling *Pteridinium* Gürich, 1930.

INTRODUCTION

The large and distinctive frond-like fossils which occur as frequent components of the Ediacara assemblage of the Flinders Ranges were first described by Glaessner (1959a). However an earlier indirect indication of these fossils was given by Sprigg (1949: p. 73), who identified some of them as algae. Glaessner (1959a) referred specimens to *Rangea* and *Pteridinium* Gürich, 1930, genera described from the Late Precambrian, Nama Group of Namibia (South West Africa) and to *Charnia* Ford, 1958, from rocks of comparable age at Charnwood Forest, Leicestershire, England. He considered these genera to be related to the living Pennatulacea. Formal descriptions of the same material were given by Glaessner (1959b) and numerous citations concerning them have appeared in his later works. Glaessner and Wade (1966) presented an updated formal taxonomic study in which they referred the then single known specimen of the *Charnia*-like form to *Rangea*, and erected the genus *Arborea* to accommodate some of the materials previously identified as belong-

ing to *Rangea*. The taxa which they recognised are as follows:—

Rangea longa Glaessner and Wade, 1966

Rangea grandis Glaessner and Wade, 1966
(single *Charnia*-like specimen)

Pteridinium cf. *simplex* Gürich, 1930

Arborea arborea (Glaessner 1959).

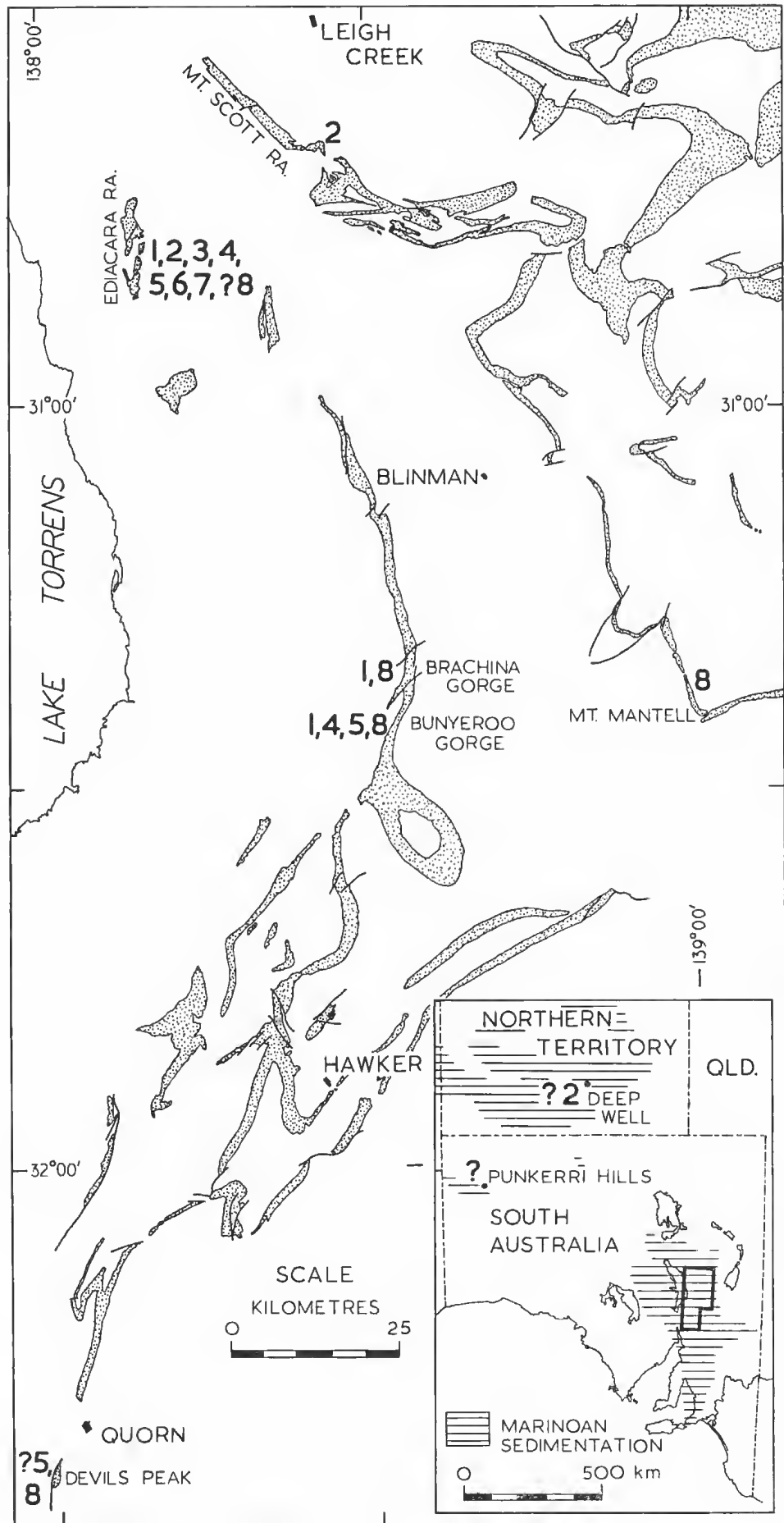
Germs (1973) considered *R. longa* and *R. grandis* distinct from *Rangea* Gürich and erected a new genus to contain them, *Glaessnerina* (type species *R. grandis*). Glaessner's (1959a, b) placement of the above listed Australian taxa as relatives of the modern octocoral Order Pennatulacea has generally been maintained in later studies (e.g. Glaessner and Wade 1966; Glaessner 1971b), although one current suggestion is that they may belong to a phylum intermediate between plants and animals, the "Petalonamae" (Pflug 1972b, c, 1973, 1974a, b). Glaessner and Walter (1975) consider that they can best be classified provisionally as Coelenterata of uncertain systematic position.

Wade (1970) reported the discovery of the Ediacara assemblage at widely spaced localities in the western Flinders Ranges and its known distribution has now been extended over much of the Ranges (m.s. in preparation). Significant, new, well preserved specimens of frond-like fossils have been found at several of these localities (Fig. 1), mainly by J.G.G. working in conjunction with Messrs. C. H. Ford and D. A. Westlake. This new material sheds additional light on the structure and probable affinities of the previously described forms and indicates a greater diversity of taxa.

Current interest has been focused on Late Precambrian, frond-like fossils by works such as those of Pflug (1970a, b, 1971a, b, 1972a, b, c, 1973, 1974a, b), and the present study has been prepared to update information on the Australian examples.

Ediacara assemblage

Termier and Termier (1960) erected the "Ediacaran" stage which they defined as being characterised by the fossils from Ediacara and the other similar "Eocambrian" fossils then



known from England and southern Africa. In a later work the same authors (Termier and Termier 1967: p. 141) discuss "la faune d'Ediacara", and subsequently they refer to the different world occurrences of the comparable fossils as "la faune ediacarienne" or "des faunes ediacariennes" (Termier and Termier 1968: p. 74 and p. 76).

The English usage "Ediacara fauna" was adopted by Wade (1970) in reference to the fossils from the Ediacara Range and elsewhere in the Flinders Ranges. Here it is considered that the term "fauna" is more applicable to the original living population of animals and that the term "assemblage" is preferable to denote the incomplete collection of fossils which, because of preservational factors, undoubtedly represents but a part of the original fauna. For example, in all of the known Australian occurrences the sand grains in the beds containing the fossils are too coarse to preserve imprints of small organisms (cf. Glaessner 1972).

Repositories

The repositories of the material studied are the South Australian Museum (registered numbers prefixed P. in text) and the Palaeontology Collection of the University of Adelaide (numbers prefixed T. or F.).

DISCUSSION

The repositories of the material studied are the fossils in the Ediacara assemblage are preserved as markings standing in either positive or negative relief on bedding plane surfaces of flaggy sandstone or quartzite. Mostly the fossils occur on the undersides of such beds. Wade (1968) detailed the several alternative ways in which they were probably preserved and indicated general principles applicable for their interpretation.

Study of the available materials referred to *Arborea* confirms that the reconstruction given by Glaessner and Wade (1966: pp. 618-620, fig. 2) is correct in its major details. They consider that the organism was basically a foliate, leaf-shaped structure normally preserved lying on one of its (two) broad sides in the plane of the bedding. This foliate structure or frond was elongate and symmetrical in form, and comprised a relatively narrow median zone or rhachis from which lateral, primary branches extended on either side

at an angle of between 45° to 90° relative to the rhachis. This interpretation is proved correct by a unique specimen (P. 19687) in which the frond is overfolded near the middle of its length so that features of both sides are preserved.

It is also evident that the primary branches were linked by a foliate base which formed one side of the frond (the more or less smooth or "dorsal" side). The branches were fleshy or inflated, and on the side opposite the foliate base (the "ventral") each supported a free standing, flap-like polyp-leaf. Each polyp-leaf shows a series of close-spaced grooves which evidently correspond to spicular supportive devices lying in the position of the joins or sutures between the polyp anthostoles. In some species the margins of the frond seem to have extended into a membranous structure or marginal-zone which was either featureless or with faint indications of extensions of the axial traces of the branches.

Frequently, the rhachis shows impressions of more or less straight spicules which were longitudinally arranged within it (Glaessner 1959a, b, 1971b; Glaessner and Wade 1966). The new materials available indicate that the rhachis continued at the base of the frond as a stalk which terminated in a disc-like structure. Such a stalk, passing into the base of a frond at one end and attached to a "bulbous expansion" at the other, is partially figured in plate 103 figure 1 of Glaessner and Wade (1966) and is discussed in the explanation of this figure on their page 624. The disc-like structure usually consists of a central circular boss and an outer flange which may or may not show evidence of a radial musculature.

Specimens of *Arborea* have been preserved with a circular collapse structure indicating the position of the buried disc in the substrate and the frond bent over and laid flat from its position in life. Thus the disc was evidently an anchoring device.

Ford (1958) described frond-like and disc-like organisms from the Late Precambrian of Charnwood Forest, England. He erected the taxon *Charnia masoni* to include most of the frond-like organisms. The disc-like structures were included in his new taxon *Charniodiscus concentricus*. Ford (1963) referred additional material to *C. concentricus*.

The holotype of *Charniodiscus concentricus* (illustrated in Ford 1958: pl. 13, fig. 2 and

Fig. 1. Locality maps of finds of Ediacaran frond-like fossils in Australia. The larger map shows the greater part of the Flinders Ranges with outcrop of the Pound Quartzite indicated by areas of stipple; numbers signify the taxa identified from each locality. 1: *Charniodiscus arboreus* (Glaessner 1959). 2: *Charniodiscus longus* (Glaessner and Wade 1966). 3: *Charniodiscus oppositus* sp. nov. 4: undescribed new species of *Charniodiscus* with crinkled resistive structures within the branches. 5: *Glaessnerina grandis* (Glaessner and Wade, 1966). 6: undescribed new species of *Glaessnerina*. 7: *Pteridium* cf. *simplex* Gürich, 1930. 8: *Phyllozoon hanseni* gen. et. sp. nov.

Ford 1963: pl. 1, fig. a) is a disc-like structure associated with a stalked frond which appears to be attached to the centre of the disc (Figs. 2 and 4). Similar Australian materials (e.g. Fig. 3) provide confirmatory evidence that the disc and attached frond represent a single organism. Ford (1963) included this frond in *Charnia*

masoni, although he previously remarked that it differed in structure from the holotype of that species (Ford 1958: pp. 213-214). The frond is of comparable dimensions to the holotype of *Charnia masoni*, but differs markedly in that it shows a wide, tapering median rhachis and has upwards of 45 branches on each side of the

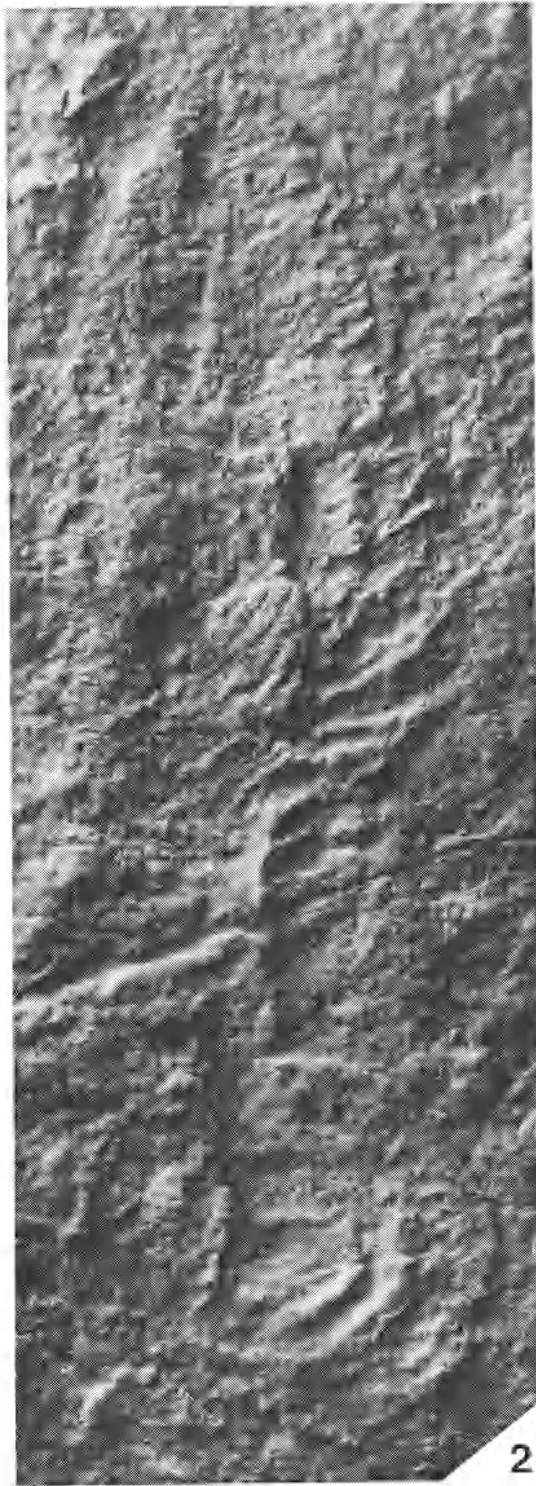


Fig. 2. Photograph of a cast of the holotype of *Charniodiscus concentricus* Ford, 1958, the original being from the Late Precambrian of Charnwood Forest, Leicestershire, England; x .8.

Fig. 3. Photograph of a cast of a specimen of *Charniodiscus arboreus* (Glaessner 1959), P. 19690, occurring at Bunyeroo Gorge, western Flinders Ranges, x .45. The zone of imperfect preservation between the disc and the base of the frond is considered to have resulted from arching of the stalk.

rhachis rather than about 20; in one area the branches show a faint cross-structure, but strong secondary divisions are lacking. The reverse side of the frond, fortuitously revealed by a small overfolded portion (Figs. 2 and 4), shows the branches to be smooth dorsally, though still delimited by weak grooves. Thus this frond cannot represent the reverse aspect of *Charnia masoni* and almost certainly represents a separate genus and species, surely referable to the available name taxon *Charniodiscus concentricus*.

The Australian Ediacara materials included in *Arborea* are extraordinarily similar to *Charniodiscus concentricus*. Their rhachis extends into a stalk attached to a quite similar disc-like structure. The number of branches is similar, upwards of 30, and there is every indication that the form of the branches and the shape of the grooves between them is comparable. The overfolded portion of the frond of the holotype of *C. concentricus* suggests that the branches were linked laterally by a foliate base. *Charniodiscus* seems to differ from *Arborea* only in that some of its branches show a pronounced curvature rather than being nearly straight. This feature may well be exaggerated by distortion.

Considering the boardly similar age of *Arborea* and *Charniodiscus* (Late Precambrian; see Glaessner 1971a) and their morphological similarity, there seems little justification in maintaining them as distinct genera and accordingly they are here considered congeneric, *Arborea* becoming a synonym of *Charniodiscus*. *Charniodiscus concentricus* can be distinguished from the local forms of the genus at the specific level.

The forms which have been included in *Arborea arborea* (Glaessner) are herein split into two separate species. *Charniodiscus arboreus* is characterised by relatively narrow branches which occur in alternate positions on each side of the rhachis; the ventral track of the rhachis is narrow and zig-zag towards the end of the frond (Fig. 3). The new taxon, described herein as *Charniodiscus oppositus* sp. nov., and illustrated in Figures 5 and 6, has broad branches situated in opposite positions on either side of the rhachis, the ventral track of which is relatively broad for its whole length.

A third and very rare form, which is new and still to be described, is tentatively included in *Charniodiscus*. It is characterised by crinkled, resistive structures within the branches. Some of these structures are bent or deformed, indicating an original flexibility.

As has already been mentioned, most of the frond-like fossils of the Ediacara assemblage are

preserved on lower surfaces of flaggy sandstone beds. The holotype of *Rangea longa* and the majority of the other specimens referred to this taxon by Glaessner and Wade (1966) are unusual in that they are preserved on the upper surfaces of quartzite slabs. Twenty or more fronds (not including the holotype, P13777) occur lying in close juxtaposition on a number of similar quartzite slabs (P12721a-i) which were evidently broken from a single bed. These fronds are all orientated in the same way, stretched out lengthwise by a current which eddied around them and scoured the sediment (Wade 1968). On the same or similar bedding surfaces (P12716, P12721b and c, P12736) are several more or less circular depressions which are evidently craters of collapse over anchoring devices resembling those described for *Charniodiscus*. An impression of part of a thick stem extends from one of these collapse craters (P12716). The organisms preserved were apparently bent over from the position in which they were anchored in life and laid flat by the current. They were gregarious, living in near proximity to one another, with individuals at all stages of growth represented.

The fronds of *R. longa* are generally preserved as external moulds, with sand underpacking spaces between the polyp-leaves and branches. No unequivocal interpretation of the structure of the frond is possible, partly because no single specimen shows a whole individual, and also because of overlapping and distortion. Nevertheless it is considered that the reconstruction of *R. longa* given by Glaessner and Wade (1966) is probably incorrect in showing polyp-leaves on both sides of the frond. The specimens interpreted as showing this (Glaessner 1959b: pl. 45 Fig. 1) include a cast (left side of figure just indicated) in which the rhachis is preserved by composite moulding. In the holotype, particularly, the structure of the frond appears to be essentially similar to that of *Charniodiscus*, with inflated, laterally linked branches each bearing a polyp-leaf. The polyp-leaves seem to narrow and terminate at the edge of the frond. It is considered that the other available specimens lend weight to those findings and accordingly *Rangea longa* is tentatively referred to *Charniodiscus*.

The frond of *R. longa* shows no evidence of a marginal membranous structure. One specimen (P12721c) seems to show the more lateral anastomoses on the polyp-leaves fanning outwards and forming a curved array at the edge of the frond, much as occurs in many modern pennatulaceans. Wade (pers. comm.) has indicated that text-figure 1c of Glaessner and Wade (1966)

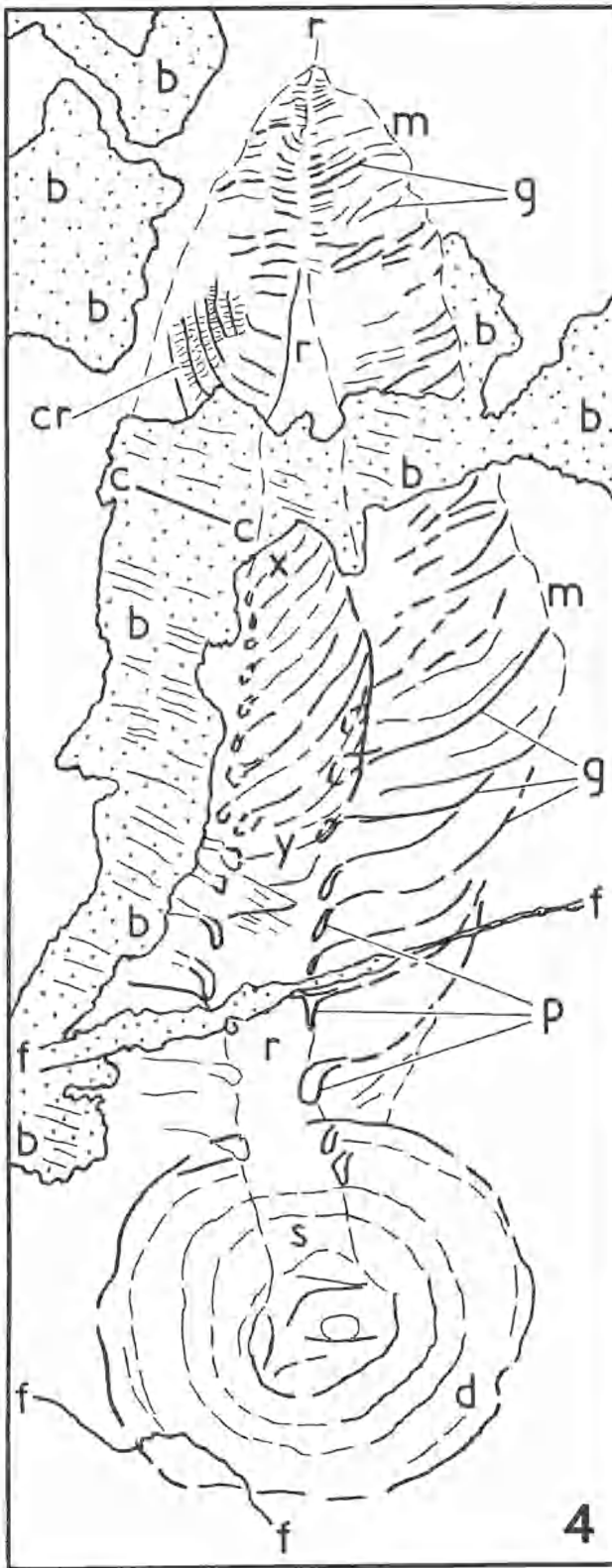


Fig. 4. Interpretive outline drawing made from the cast of the holotype of *Charniodiscus concentricus* Ford, 1958, illustrated in figure 2; x 08 f, fractures in original rock surface; b, projecting irregularities in sediment; d, disc of organism and, s, stalk attached to it; r, rhachis of frond; m, outline of frond; g, primary grooves between branches of frond and p, pockets formed by these grooves adjacent to the rhachis; cr, faint cross-structure on branches; x-y, overfolded portion of frond.

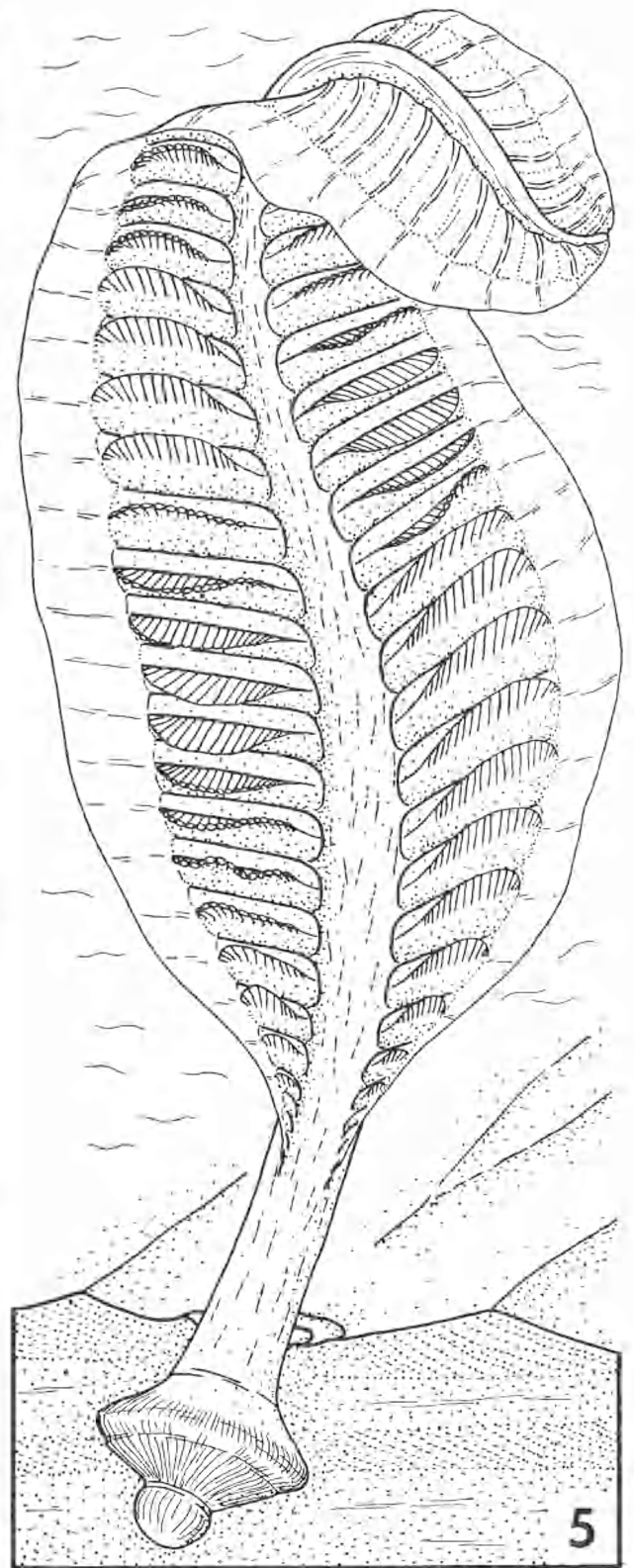


Fig. 5. A reconstruction of *Charniodiscus oppositus* sp. nov., about x .8 of average sized specimens. The organism is shown in its inferred life position, anchored in ripple-bedded sands. It is drawn as though it were partly transparent, the spicules shown in the stalk and rhachis were evidently imbedded in the sub-dermal integument.

is based on similar evidence, but we consider that the polyp-leaves only overlapped or enveloped one another to a minimal degree.

The genus *Glaessnerina* Germs, 1973, is considered herein to include its type species *Rangea grandis* Glaessner and Wade and one other new species yet to be described. *Glaessnerina grandis* is now represented by four specimens, three of which show the polyp-bearing ventral side of the frond, and the other the dorsal side, which is characterised by a broad rhachis (P, 19688). The branches of its frond were evidently attached to the ventral side of the rhachis. The polyp anthostoles on one branch reached to or overlapped those of the next serial branch on the opposite side to completely hide the rhachis and give the effect of a zig-zag medial commissure. This overlap of the polyps is probably a function of compression during preservation, as in life the polyps must have projected away from the frond at an angle so that there was no interference between them during feeding.

Little new information can be added concerning the form which Glaessner (1963) and Glaessner and Wade (1966) identify as *Pteridinium* cf. *simplex* (Gürich 1930). The majority of specimens are unusual in that they are preserved as moulds and counterpart moulds in massive sandstone (Wade 1968, 1971). These fossils provide no indication as to how the organism may have been oriented relative to bedding, much less its possible orientation in life. Pflug (1970a, b, 1971a, b, 1972a, 1973) has now given an extensive documentation of the material of *Pteridinium* from the Nama Group of Namibia. Their preservation is evidently the same as for the Australian examples. The African specimens often show three half leaf-shaped elements ("petaloids" of Pflug 1970a) extending from an axial line. One of the Australian specimens (plate 101, figure 1 of Glaessner and Wade 1966) also shows three petaloids extending from the axis, two of the petaloids lying in close juxtaposition and separated by a thin lamina (about 1 mm thick) of quartzite, and the third more or less symmetrically opposite, on the other side of the axial line.

A new taxon, *Phyllozoon hanseni* gen. et sp. nov. is erected for a leaf-shaped fossil, numerous individuals of which are typically preserved together on lower surfaces of quartzite beds. The frond of this organism shows numerous distinct grooves extending away from a zig-zag median suture, and appears to have had a membranous or foliate base. The lateral grooves extend from the axis of the frond at 65° to 85°

and gradually become more widely spaced in the direction of the end of the frond towards which they are inclined. It is evident that the median axis of the frond and the lateral grooves actually represent a flexible, resistive framework or skeleton. The edges of the frond are usually indistinct.

Specimens of frond-like fossils have been reported from the northern part of the Officer Basin in the possibly Late Precambrian Punkerri Beds of the Punkerri Hills, northwestern South Australia (Major 1974 and references therein). Restudy suggests that one of the supposed remains is of inorganic origin, a pseudofossil of striking realism simulated by a set of repeated parallel micro-faults. Imprints on another block of sandstone resemble parts of the frond of *Charniodiscus*, but are so fragmentary that they should be considered essentially indeterminate.

The above discussion, together with more detailed studies too lengthy to be included in this work, provide the basis for the systematic listing below.

SYSTEMATICS

Genus *Charniodiscus* Ford, 1958

Type species:

Charniodiscus concentricus Ford, 1958: 213, pl. 31 fig. 2, by monotypy.

Charniodiscus Ford, 1958: 213; 1963: 57. *Rangea* Gürich, 1930. Glaessner, 1959a: 1472-1473; 1959b: 383. Glaessner and Wade, 1966 (partim): 614-616.

Charnia Ford, 1958. Glaessner, 1962: 483 (partim, with reference to pl. 1 fig. 5).

Arborea Glaessner and Wade, 1966 (partim): 618-619.

Revised diagnosis: Frond large, leaf-like, fusiform or tapering; dorsal track of rhachis wide, ventral track narrower, either straight or tapering narrowly and zig-zag, base of rhachis forming a stalk attached to centre of a disc-shaped structure showing a central circular boss and an outer flange which may have a radial ornament; branches about 30 to more than 50 in number (on either side of frond) situated either in alternate or opposite positions along rhachis and diverging from it at 45° to 90°; individual branches evidently swollen or inflated during life, composed largely of unresistant material, but generally with a stiffened or resistant structure positioned medially; each branch linked to immediate neighbours by a foliate base, and with

grooves between, these grooves curved and particularly deep near rhachis; mature branches each bearing a flap or flange-like polyp-leaf which shows secondary grooves delimiting fused polyp anthosteles; edges of frond either with or without a membranous marginal one.

Referred taxa: The Australian forms which are apparently referable to this genus are all evidently of Late Precambrian age and are as follows:

Rangea arborea Glaessner, 1969, about 30 specimens from the Pound Quartzite and occurring variously at Ediacara Range, Brachina Gorge and Bunyerroo Gorge, in the Flinders Ranges. The holotype is specimen P. 12891, and two paratypes are P. 12892 and P. 12895; other referable specimens are P. 13787, P. 13801b, P. 14212, P. 19689, and F. 16718; all from Ediacara Range. A cast of a specimen occurring at Bunyerroo Gorge, P. 19690, is shown in Figure 3.

Rangea longa Glaessner and Wade, 1966, approximately 30 specimens from the Pound Quartzite, occurring mainly at Ediacara Range, but with one specimen from Mount Scott Range (coll. Dr. B. Daily), Flinders Ranges. The holotype is specimen P. 13777, with the paratypes including P. 12716, P. 12721 a-i, P. 12736 and P. 12743; all from Ediacara Range. Also referable to *Charniodiscus* is a specimen of a small part of a frond collected in a loose block on the lower part of the Arumbera Formation, east of Deep Well Homestead, S.S.E. of Alice Springs, central Australia, and identified by Glaessner (1969) as *Rangea* cf. *longa*. Restudy of the specimen suggests that it is too incomplete for specific identification.

Two new species from the Pound Quartzite of the Flinders Ranges; one represented by more than 40 specimens and described below; the second very rare and yet to be described (see p. 351 above).

Charniodiscus oppositus sp. nov.
Figs. 5 and 6

Rangea sp. Glaessner, 1959a (partim): 1472-3.

Rangea arborea Glaessner, 1959b (partim): 383, pl. 43 figs. 2 and 4, pl. 44 figs. 1 and 3. Glaessner, 1961 (partim): fig. p. 75; 1962 (partim): 483-485, pl. 1 fig. 10.

Arborea arborea (Glaessner 1959). Glaessner and Wade, 1966 (partim): 619.

Derivation of name: From the Latin *oppositus*,

in reference to the approximate opposite positioning of the branches on either side of the rhachis.

Diagnosis: Species reaching large size with frond up to 30 cm wide and well in excess of 73 cm long; frond broad, 2.5-4 times as long as wide in more complete specimens (excluding marginal zone); ventral track of rhachis wide, only slightly narrower than the dorsal; branches about 30 in number (on each side of frond), located in nearly opposite positions on either side of rhachis and diverging away from it at about 65° to 85°; branches relatively broad, 3.3-5 times as long as wide on more central parts of frond.

Material: This is one of the more numerous frond-like fossils in the Ediacara assemblage with upwards of 40 specimens being referable to it with greater or lesser degrees of confidence. The holotype is F. 17337 and the nominated paratypes are T. 94-2015, T. 94-2016, P. 12888, P. 12896, P. 14213, P. 19684, P. 19685 and P. 19687; all from Ediacara Range. Also referable is a specimen occurring at Bunyerroo Gorge and represented by a cast, P. 19686.

The majority of specimens are preserved as casts (sometimes with composite moulding) on the bottom surfaces of sandstone flags. The holotype is uniquely preserved as a smooth external mould within a sandstone bed (Fig. 6).

Remarks: *C. oppositus* closely resembles *C. concentricus*, but differs in that its branches do not show a pronounced trend to decrease in width towards the tip of the frond and are possibly less numerous. The well marked radial ornament on the outer flange of its attachment disc may also be distinctive.

C. oppositus differs from *C. arboreus* in the more regular width of its branches and in their opposite rather than alternate positioning on either side of the rhachis. The attachment disc has a smaller central boss relative to *C. arboreus*. *C. longus* has a much more elongate frond with very numerous branches.

Zoological affinities: Glaessner (1959a, b, 1961, 1962, 1963, 1969, 1971a, b) and Glaessner and Wade (1966) considered that the frond-like fossils of the kind just described are allied to living members of the order Pennatulacea. The few difficulties which the above authors raised against this interpretation are now largely obviated by information from the new materials for *Charniodiscus* to hand and studies of modern live pennatulids (e.g. Brafield 1969, and observations made by J.G.G. on living animals on the sea floor and in aquaria). Some major charac-

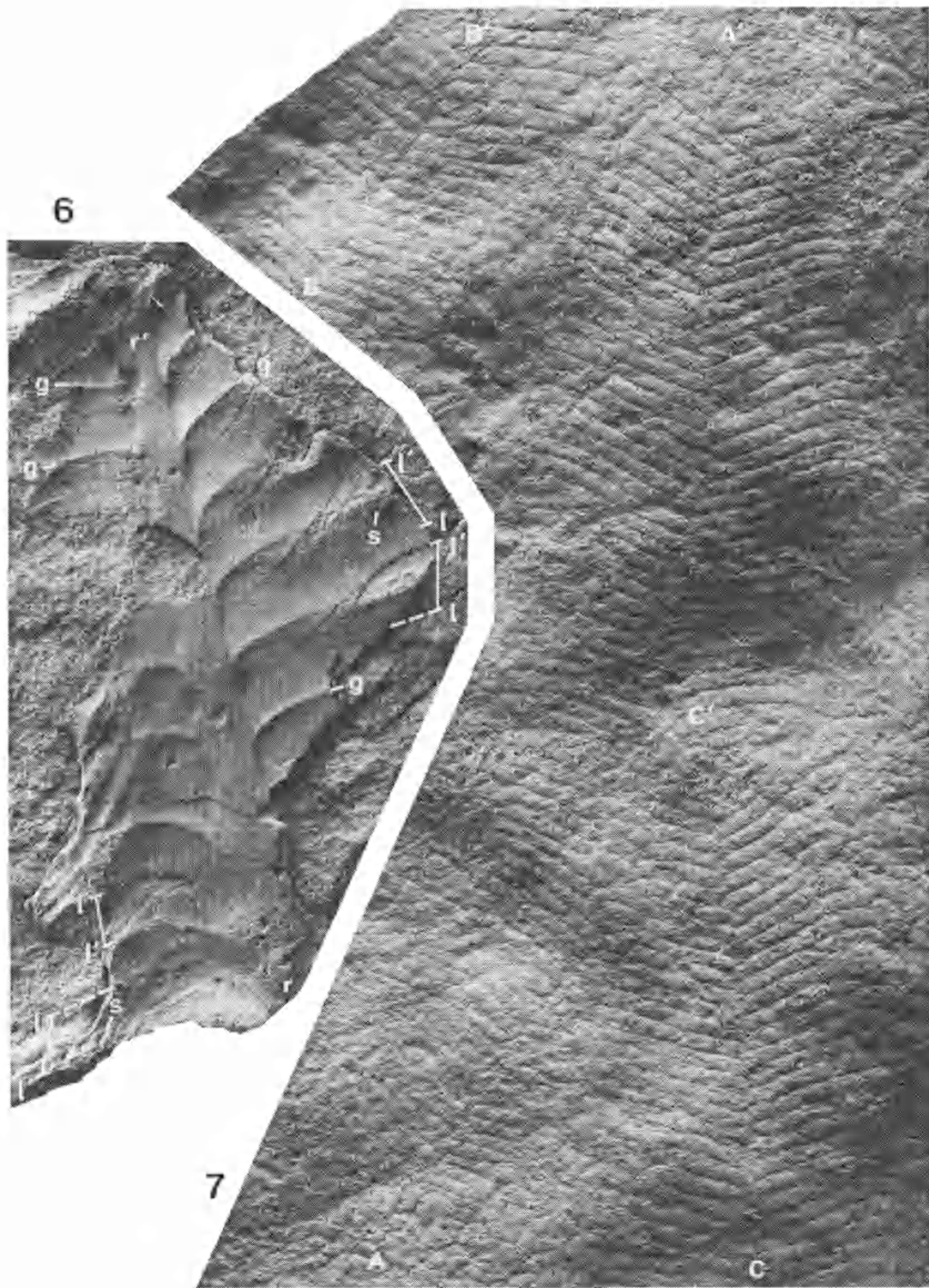


Fig. 6. Holotype of *Charniodiscus oppositus* sp. nov., F.17337, from Ediacara Range, x 7. The specimen is an external mould of a central part of the polyp-bearing (ventral) side of the frond. r, r', rhachis; g, grooves between the primary branches; l-l', flap-like polyp-leaves extending distally on the right side of the frond and folded proximally on the left side; s, spicular supportive devices in the polyp-leaves.

Fig. 7. *Phyllozoon hansenii* gen. et sp. nov. Holotype, specimen A-A', P.19508A, and incomplete remains of two paratype specimens, B-B' and C-C', from the Devils Peak, southern Flinders Ranges, x 1. Composite moulding has occurred where the end of specimen C-C' overlaps the holotype, A-A'.

teristics shared by *Charniodiscus* and present-day pennatulaceans are as follows:—

- a. Both have an anchoring structure characterised by strong longitudinal or radial musculature. In the living genus *Ptereoidea* Herklots, 1858, the anchoring device is essentially a muscular sack which can be dilated with water. A sphincter muscle lies at the junction of this sack and the stalk. A basal expansion or protrusion of the sack (Brafield 1969: pl. 1, fig. a) seems analagous to the central boss in the attachment disc of the fossil forms.
- b. A stalk and median rhachis is present in each. In modern pennatulaceans the rhachis functions as a hydrostatic organ of support, becoming greatly swollen and stiffened by water drawn into large internal canals; in symmetrical forms additional support is provided by a calcified rod or axis in the lower part of the rhachis and stalk. *Charniodiscus* lacked this rod or axis; its rhachis, though up 3-4 cm wide in large specimens, readily collapsed flat during preservation, suggesting that it was also filled largely with fluid during life.
- c. Spicular elements present in the stalk and rhachis of *Charniodiscus* resemble those commonly occurring in the modern animals.
- d. In both, lateral branches extending from the rhachis bear foliate structures (polyp-leaves) showing secondary divisions (polyp anthosteles). The branches of modern forms can be inflated with water and some specimens of *Charniodiscus* also show evidence that the branches were dilated.
- e. The large spicules evident in the polyp-leaves of *Charniodiscus* seem analogous with those in species of *Pennatula* Linné, 1758, and *Ptereoidea*.
- f. Modern pennatulids, even those with an axis, have considerable powers of distension and contraction. A live specimen of *Ptereoidea* has been observed to extend its length by about 100 per cent from the contracted to the expanded state. Specimens of *Charniodiscus* showing evidence of appreciable stretching by currents suggest that it also may have been capable of significant distension.

Charniodiscus was seemingly close to the living branched family Pennatulidae in its gross morph-

ology, but differed in lacking a calcified axis and in having its branches fused or linked laterally rather than free. The extant Renillidae have a continuous foliate frond and no axis, but lack recognisable branches. Considering the diversity of form shown by modern pennatulaceans and their very long separation in time from the Ediacara assemblage, it is hardly surprising that *Charniodiscus* shows several unique characteristics.

Genus *Glaessnerina* Germs, 1973

Type species: *Rangea grandis* Glaessner and Wade, 1966: 616, pl. 100 fig. 5, by original designation.

Glaessnerina Germs, 1973: 5.

Revised diagnosis: Frond large, tapering, with broad tapering dorsal rhachis; primary branches situated in alternate positions on rhachis and diverging from it at approximately 40-65°, with their lateral terminations sharply delimited; each primary branch bearing a row of large, similar, blunt secondary branches (polyp anthosteles) projecting obliquely towards axis of frond at about 30-50° to it; secondary branches of type species widest near rhachis and becoming progressively narrower away from it; basal parts of primary branches and secondary branches overlapping in ventral midline to form a zig-zag commissure.

Remarks: In a number of his earlier works on the Ediacara assemblage Glaessner (1959a, 1959b, 1961, 1962) referred the type species of this taxon, *Rangea grandis*, to the genus *Charnia*. Germs (1973) again drew attention to the similarity between *Glaessnerina grandis* and *Charnia* and suggested that further study of them might "make it advisable to place them in the same genus". However, several marked differences do occur between them and for this reason their separation is maintained here.

In *Glaessnerina* part of each primary branch is continuous or undivided, and it is this undivided portion which bears the secondary branches. In *Charnia*, the secondary divisions extend continuously across the primary branches, and as well, have their long axis more nearly transverse to the axis of the whole frond. The secondary divisions of the branches of *Glaessnerina* are widest near the axis of the frond and become progressively narrower towards the ends of the primary branches. The secondary structures of *Charnia* are narrow near the frond axis, become wider near the middle of the length of each primary branch, and then narrow again towards the edge of the frond. A further distinctive character in

Charnia is that the secondary structures are themselves regularly subdivided by tertiary grooves.

In its morphology *Glaessnerina* shows a resemblance to *Charniodiscus* on the one hand, and a suggestive similarity to members of the extant Pennatulidae on the other. It is almost certainly related to *Charniodiscus* and thus can also probably be considered as allied to the pennatulaceans.

Genus *Pteridinium* Gürich, 1930

Type species: *Pteridinium simplex* Gürich, 1930: 637, by original designation.

Interpretations given to this genus by Pflug (1970a, b, 1971a, b, 1972a, 1973) pose problems outside the scope of the present work, and it seems inappropriate to attempt to provide a generic diagnosis.

Referred taxa: The single Australian form is represented by rare materials from Ediacara which Glaessner (1963) and Glaessner and Wade (1966) identify as *Pteridinium cf. simplex*. Aside from the brief remarks above on pp 353 no new information can be given.

Genus *Phyllozoon* gen. nov.

Type species: *Phyllozoon hansenii* sp. nov.

Derivation of name: *Phyllo*, from the Greek noun *phyllon*, leaf; *zoon*, Greek for animal.

Diagnosis: As for type species.

Phyllozoon hansenii sp. nov.

Fig. 7

Derivation of name: The species is named after Mr. Anthony Kym Hansen, who made the initial discovery of this taxon whilst studying geology at Adelaide University, and has since lost his life during seismic exploration in Western Australia, 1976.

Diagnosis: Frond leaf-like, resembling *Pteridinium simplex* in its incised zig-zag median line and almost evenly spaced, repetitive lateral grooves, but differing in that the organism was evidently of more or less planar or two dimensional form, not with three ribbed wings extending from the axis; incised axis and lateral grooves evidently representing a resistive skeleton which lay within foliate base of frond; lateral grooves extending from axis at about 70°, with their ends curved outwards; spacing of lateral grooves tending to become less at (?) proximal end of frond.

Material: Fifteen or so individuals are available for study. The holotype, P. 19508A, a nearly complete frond, and eight or nine other frag-

mentary individuals, all occurring on a single bedding plane, were discovered by Mr. A. K. Hansen at Devils Peak, southern Flinders Ranges. Three individuals occurred at Mt. Mantell Range, central Flinders Ranges. Numerous individuals have been observed on rock slabs in the Heysen Range, western Flinders Ranges, particularly near Bunyeroo Gorge; a specimen occurs in a collection from Brachina Gorge. Several fragmentary remains showing resemblances to this taxon are present in collections from Ediacara.

Dimensions: The frond of the holotype (specimen A, A' in Fig. 7) is about 18 cm long and 5.5 cm wide towards the middle of its length, with about 75 lateral grooves (on each side of frond) spaced at about 2 mm (end of frond opposite to direction in which lateral grooves are inclined) to fractionally under 3 mm (average). A spacing of about 3 mm is common in other specimens. Individuals may reach in excess of 23 cm long with upwards of 100 lateral grooves.

Remarks: *Phyllozoon hansenii* apparently differs from the Namibian material of *Pteridinium simplex* in that it is a two dimensional frond, showing no evidence of an additional ribbed wing extending from the axis. Where separate, individual fronds overlap, composite moulding results, and if an additional wing did exist it seems likely that it would be evidenced by this process. Another difference between the new form and *P. simplex* is that the lateral grooves show a characteristic inclination relative to the axis (about 70°) in the former, but are nearly transverse or variably inclined in the latter. *Phyllozoon* does not show a series of small distinct lobes adjacent to the axis, a character often present in *Pteridinium* (where they have been termed "commissurae" by Pflug, 1970a).

P. hansenii differs from the material from Ediacara identified as *Pteridinium cf. simplex* in that the ends of its lateral grooves curve in the opposite direction and do not converge together towards the margin of the frond, and "commissurae" are lacking.

P. hansenii shows a resemblance to another of the forms occurring in the Nama Group, *Nasepia altae* Germs, 1973. The latter is described as consisting of ribbed, leaf-like bodies (petaloids) which have a "skeletal structure". However, a number of petaloids are evidently bundled together in *Nasepia* and the individual petaloids seem to be broad rather than elongate in shape.

A striking, but probably superficial similarity of form exists between *P. hansenii* and species of *Plumalina* Hall, 1858, frond-like remains occur-

ring in the Middle Devonian to latest Devonian or earliest Mississippian of New York and the Middle Devonian of Eifel, Germany. In the detailed recent review of *Plumalina* presented by Sass and Rock (1975) it is described as being a plume or feather-like form, in which the separate lateral branches (or "pinnae") and perhaps the rhachis were apparently tubular prior to burial. *P. hanseni* differs from *Plumalina* principally in having a foliate base to the frond rather than separate pinnae, and in its axial line consisting essentially of a single groove, not a distinct narrow band forming a clearly marked rhachis.

In their discussion of the likely affinities of *Plumalina*, Sass and Rock reject the possibility that it is a plant and compare it to members of the Gorgonacea and hydrozoans belonging to the feather-like Plumulariidae. In the last paragraph of their work they favour an affinity with the hydrozoa, a view with which we concur.

In the Plumulariidae and near relatives (members of the Order Hydrozoa) the colony consists of an axial stolon or hydrocaulus from which branch individual lateral stolons bearing small or microscopic polyps or hydranths (Hyman 1940). The stolons have a chitinous covering or periderm; the polyps are partially enclosed by goblet-shaped expansions of the periderm, the hydrotheca. The colony grows by the progressive budding and branching of new single stolons from the distal end of the hydrocaulus. This mode of development would seem to preclude the evolution of a common membrane inter-connecting the individual branches of the frond. Thus it seems unlikely that *Phyllozoon* is allied to the Plumulariidae and there is a dearth of evidence to link it with other hydrozoans.

In the short recent review which Glaessner and Walter (1975) present on the now diverse array of frond- and sack-like fossils variously known from a number of Late Precambrian localities in the world, they consider that these remains all show a "general similarity" and imply that this reflects an underlying taxonomic unity. This viewpoint may, however, prove to be simplistic.

As has been argued above, the genera *Charniodiscus* and *Glaessnerina* and probably *Charnia* are evidently allies of the modern Pennatulacea. On the other hand, the unnamed Late Precambrian forms from Newfoundland which Glaessner (in Glaessner and Walter 1975) considered as possibly being allied to hydrozoans, show a pattern of branching consistent with this hypothesis. A comparable form of branching is present in *Rangaea* (see Pflug 1970b; Germs 1973). A quite different phylum may be repre-

sented by the apparently sack-like form *Arumbera banksi* Glaessner and Walter, 1975, which is a relatively common fossil in the latest Precambrian of central Australia. Its walls are characterised by a skeleton of elongate, subparallel, resistive fibrils, and the form shows a suggestive resemblance to primitive, thin-walled, vase-shaped sponges, such as the Early Palaeozoic Leptomitidae.

The possible systematic position of genera such as *Pteridinium* and *Nasepia* and the remaining forms grouped in the "Petalonamiae" is clouded, either because of imperfect preservation, or inconsistencies in presently available descriptions. There is apparently little recorded field information which might throw light on either their life habits or life orientation. The resemblance which *Phyllozoon* shows to *Pteridinium*, together with its enigmatic state of preservation, dictate its present placement within this essentially unclassified group.

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